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Genetic and environmental factors influencing gain and fatness in swine

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GENETIC AND ENVIRONMENTAL FACTORS INFLUENCING GAIN AND FATNESS IN SWINE

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I. INTRODUCTION

Progress through selecting superior genetic material is a function of the genetic variability in the population, the intensity and accuracy of the selection and the genetic and environmental correlations existing among the traits under selection. Little can be accomplished, without inbreeding or wide outbreeding, toward altering the amount of genetic variability within a population. The most practical possibility of achieving greater genetic progress lies in improving the accuracy of the selection practiced. This will require as complete knowledge as possible of the genetic and environmental relationships among the traits to which selection is addressed.

Knowledge of the properties of Mendelian populations has furthered the designing of new devices and procedures to increase the accuracy of selection. Information on the progeny and the collateral relatives of individuals, use of correlated traits and the combining of this knowledge into selection indexes all have been used as aids in attempts to identify the superior genotypes. The choice of the most effective method in a given situation depends on understanding correctly the nature and structure of the environmental and genetic forces operating within the population.

Central testing facilities to evaluate the economic traits of swine have been in operation for many years in several countries. Notable examples are the testing programs in the Netherlands, Denmark, Sweden and Canada. This testing has been employed to further the genetic improvement of swine. More recently a similar testing program was

inaugurated in Iowa. A knowledge of the forces which influence the expression of the traits under test conditions is useful in developing efficient testing procedures.

Considerable evidence is available on the genetic and environmental parameters related to the economic characteristics of swine. Central testing enjoyed a brief popularity in this country during the early Thirties and has recently regained prominence in many areas. The possible genetic consequences of central testing programs on an entire swine population can not be forecasted accurately until adequate data has been accumulated from the population involved. All central testing procedures have been faced with similar problems. The questions which almost invariably arise include the effects of pre-test environment on the ultimate expression of the traits and the extent that selection of individuals to be tested influences the results of the program.

One of the objectives of this study was to measure the environmental sources of variation in daily gain and live probe of swine sent by breeders to a central testing station. Furthermore, the influence of pre-test environment on the expression of these traits in the testing station was studied. The nature and effect of the breeders' selection of individuals sent to the testing station was evaluated. Finally, an attempt was made to acquire a more complete knowledge of the nature of the genetic variability in the population.

II. REVIEW OF LITERATURE

The analysis of testing station results presents problems which are somewhat different than those encountered in studies of individual and experimental herds. Genetic parameters obtained from testing station results have often been subjected to confounding environmental influences. Factors such as pre-test environmental influences and selection of test animals are often important issues in the analysis of the testing station data. Even where these biases are recognized, the structure of the data sometimes may preclude their estimation.

The influences of yearly differences and the effects of season differences within years are widely recognized as possible major sources of variation in growth rate and carcass characteristics. Lush (1936) found important yearly influences on gain and backfat in the analysis of the Danish testing work. Fredeen (1953) attributed most of the station influence on the age at slaughter of over 12,000 pigs in the Canadian data to seasonal differences within years coupled with an unequal distribution of test litters at various stations over the year. Sutherland (1958) found that seasons contributed to an important part of the total variance in gain and probe in the first three seasons of data from the Iowa testing station.

Breed differences are similarly recognized major sources of variation among traits of swine. Johansson and Korkman (1950), in Swedish material comprising 3036 test groups of four pigs each, found that six and seven per cent of the total variance in gain and backfat, respectively, arose through differences between the Swedish Landrace and Large

White breeds. Ollivier (1957) found real breed differences in growth rate and carcass characteristics in 601 purebred and crossbred pigs from the Iowa Experiment Station. Sutherland (1958) found breed differences in gain and especially in probe for the nine breeds under test at the Iowa testing station.

Almost without exception the effects of years, seasons, and breeds have been important for growth rate and carcass characteristics such as backfat thickness. These influences must be considered in any analysis of these characteristics in swine.

Separating the total variance for daily gain and backfat thickness into genetic and environmental portions has been accomplished in many separate studies. Gain has been measured in different ways and over different ages. The phase of growth measured in this study covers the period from immediately after weaning to 200 pounds. During the first part of the period increases in weight are mostly in skeletal and muscular structures while the deposition of fat occurs during the later part of the period (McMeekan, 1938). The physiological causes of some of the genetically determined growth differences in swine were investigated by Baird, et al. (1952). The amount of pituitary growth hormone was significantly larger in fast-gaining swine than in the slow-gaining individuals.

Estimates of the heritable portions of the total variance of daily gain have usually been between twenty and thirty per cent. Lush (1936), combining several estimates of heritability from data of the Danish testing systems, found daily gain to 200 pounds to have a heritability

of 0.24. Nordskog, et al. (1944) found 0.21 for the heritability of gain from weaning to 200 pounds. They used the intra-sire regression of progeny on dam in data on 320 litters. Dickerson (1947) analysed the gains of Poland China and Landrace pigs and, from the paternal sib correlation, obtained 0.31 for heritability. There were 62 degrees of freedom for sires in this study.

The difficulties involved in separating the environmental correlations from the genetic portions of the paternal sib correlation have been emphasized in several studies. The work of Johansson and Korkman (1950) and of Fredeen (1953) on the results of central testing in Sweden and Canada, respectively, both mention this problem. In these studies the heritability of age at slaughter, a measure of daily gain, was nearly 0.60. The data were extensive in both cases but the heritability appeared to be biased upward. The fact that all the individuals in a sire group had a common pre-test environment was a recognized but unestimable source of error. Sutherland (1958) found similarly high estimates of heritability, 0.85, from the paternal sib correlation for daily gain in data from the Iowa testing station. Since the average farm or pre-test environmental influences seemed not to contribute to the total variance in gain in his study, the reason for the high heritability estimate was not altogether certain.

The maternal environment appears to contribute from ten to twenty per cent of the total variance in post-weaning growth. Dickerson (1947), for example, ascribed sixteen per cent of the variance in gain from 56 days to slaughter to the common litter environment. In all studies of

daily gain the variance within the litters appears to be responsible for over half the total variance.

The measurement of backfat thickness by live probing techniques is comparatively recent (Hazel and Kline, 1952), so that most studies of backfat thickness are based on carcass rather than live measurements. While the two measurements are not identical they are highly correlated.

Carcass traits such as backfat thickness are, in general, more highly heritable than growth characteristics. The thickness of backfat appears to have a heritability near fifty per cent. The value in Danish Landrace was given by Lush (1936) as 0.47. The paternal sib correlation yielded an estimate of 0.54 in a study by Dickerson (1947). Johansson and Korkman (1950) found 0.52 for the heritability of backfat thickness in the Swedish testing program. However, Sutherland (1958) found from the first three seasons of data taken on the Iowa testing station that conventional methods of estimating heritability of live probe gave answers greater than unity even after the effects of pre-test farm differences were presumably removed. Factors appeared to be operating in the results of the Iowa testing program to inflate considerably the estimates of genetic parameters other than the pre-test farm environments.

Carcass traits are less influenced through maternal environment than the growth traits. Usually less than ten per cent of the variance in carcass traits can be identified with the common litter environment. Fredeen (1953), for example, found eight per cent of the total variance

in backfat thickness was ascribed to the effects of maternal influences and the dominance and epistatic components that are associated with the variance between litters by the same sire.

Previous studies in swine have generally dealt with the possible biases included in using the paternal sib correlation to estimate the additive genetic variance. The environmental factors which are often confounded with sire are probably the most serious bias. Unfortunately, it is not always possible to determine the extent of such biases. The paternal sib component, if it were free of environmental correlations and epistatic effects, would allow an unbiased estimate of the additive variance when divided by the average relationship between paternal sibs.

The common procedure is to divide the paternal sib component by 0.25 which is valid where there is no inbreeding and the dams mated to a particular sire are unrelated. The later assumption, under conditions where the swine are from the herds of individual breeders is seldom realistic. In the studies of Danish Landrace by Lush (1936) and Canadian Yorkshire by Fredeen (1953) the authors assumed what appeared to be reasonable values for the average relationship within sire groups. For example, Fredeen (1953) considered the average relationship between sows mated to a particular boar was approximately that of half sister. Johansson and Korkman (1950) computed from pedigree studies a value of 0.225 for the average relationship between dams in the Swedish data, which is slightly less than the estimate given in the Canadian work. In the analysis of swine data from

individual herds, some allowance must be made for the average relationship of sows within these herds or the estimated heritable fraction from the paternal sib correlation will be too large.

The correlations, phenotypic and genetic, between daily gain and backfat thickness have generally been studied when estimating the heritability of these traits. The phenotypic correlation between these traits is about 0.2. The genetic correlations reported in the literature vary widely but are generally in the same direction but smaller than the phenotypic relationship. Blunn and Baker (1947) gave values of 0.29 and -0.04 for the phenotypic and genetic correlations, respectively, between gain and backfat thickness in Durocs. Dickerson (1947) found a phenotypic correlation of 0.10 between the traits but an extremely high genetic correlation, 1.34, when he used the components of variance and covariance ascribed to paternal sibs. Johansson and Korkman (1950) in Sweden computed a low positive phenotypic correlation and a slightly negative genetic correlation between gain and backfat thickness. Sutherland (1958) found 0.27 and 0.38 for the phenotypic and genetic correlations, respectively, between gain and live probe, using paternal sib components.

Genetic correlations calculated from paternal sib components will, of course, be biased by the incomplete removal of the environmental portions of these components. Such environmental correlations will almost always increase the components of variance but may move the components of covariance in either direction. Thus, estimates of genetic correlation must be regarded with at least the same caution

as estimates of heritability, especially when environmental confounding is suspected. In addition, estimates of genetic correlation are plagued with high sampling errors.

When the choice of animals to be tested is left in any manner to the discretion of the individual breeders some account must be made of the effects of selection on the results obtained. The difficulties of correcting for such selection led the Swedish authorities to take the choice of test pigs out of the hands of individual breeders and place it under the control of the testing officials. Johansson and Korkman (1950) investigated the representativeness of the test groups as a sample of their litter. The variability in weaning weight among the test pigs was distinctly less than that in the whole litter and the average weaning weight was significantly higher in the test groups. Selection appeared to have influenced the weaning weight. Rather surprisingly, official control did not reduce the intensity of the selection. A further study of these data did not demonstrate clearly that the intensity of selection increased with the litter size although this would be expected.

The methods and meaning of partitioning the total genetic variance into components of additive genetic variance, intra-allelic and inter-allelic interactions has been developed by Fisher, Wright, Haldane and others during the forty years since the publication of Fisher's paper in 1918 dealing with the correlations between relatives. More recently the work of Cockerham (1954) and Kempthorne (1954) has clarified the partitioning of genetic variance in the presence of epistasis and has demonstrated the similarities of the methods to those used to subdivide

the sums of squares in ordinary factorial experiments. Considerable difficulties are attached to estimating the importance of various fractions of total genetic variance. Several possible approaches to the problem have been discussed by Kempthorne (1957).

Whatley (1942) analyzed the average variance within groups of pigs having a specific relationship. The linear regression of the variance in 180-day weight on the relationship provided an estimate of additive variance. The relationships extended above that of full sibs since the population included some partially inbred lines. He thus estimated the additive variance in weight to be 30 per cent of the total variance.

The problem of how to estimate other components, as well as the additive fraction, was undertaken by Freeman (1957), using the records from New York dairy cattle. Many computational difficulties were encountered, aside from the problems of removing the various environmental correlations from the covariances of related groups of animals. Many of the relationships were very low which gave high sampling errors to the estimated components.

Gathering enough data concerning large animals to give even moderate stability to estimates from such partitioning of genetic variance is not a simple task. Computation of the coefficient of the relationship is often difficult. The problems concerning possible environmental correlation are compounded in studies of this nature because of increasingly large sampling errors. The problems of the importance of additive, dominance and epistatic variance, the degree of dominance and the extent and nature of maternal influence are such that considerable

time and many separate studies will be required to obtain dependable answers.

III. DATA

A. Source and Characteristics

Data for this study came from the records of the Iowa Swine Testing Association which operates a central testing station near Ames. The station was started in the spring of 1956 and has conducted two tests each year since that time. Spring-farrowed pigs are tested mainly during May, June and July while the fall-farrowed pigs are tested mainly during November, December and January. The results of all tests from the spring of 1956 to the spring of 1958 were the source of the data used in this study.

The requirements for testing pigs in the station were changed after the first two tests; hence the data fall into two rather distinct categories. In the first two tests during the spring and fall of 1956 each entry consisted of six pigs, two barrows and four boars, from a swine breeder located in Iowa. Each entry was housed in two pens, one barrow and two boars being assigned at random to each pen. Since the station has a total of 102 pens, this allowed 51 entries in each of the first two testing seasons.

In the next three tests, spring and fall of 1957 and spring 1958, each entry consisted of four pigs, one barrow and three boars, fed in a single pen. This arrangement allowed 102 breeders to participate during each season. The total information used in this study came from 1266 boars and 467 barrows of nine breeds, fed in five separate test periods.

The traits studied were daily gain and depth of backfat. The gain per day was obtained by dividing the total pounds of gain by the total days on test. The thickness of backfat was measured in tenths of an inch. The six live probe measurements made on each pig when it weighed approximately two hundred pounds were averaged and this average was adjusted for variation in live weight by factors developed by Durham and Zeller (1955). This adjusted average probe was the unit for a particular pig in all subsequent computations.

Several features in the nature and structure of the data deserve emphasis. First, since all the pigs from a particular farm are required to be paternal sibs, the genetic differences between sires are confounded with any environmental and genetic differences between farms. Sire and pen differences were confounded in the last three seasons since all the pigs of an entry were kept in the same pen. Secondly, the pigs may have been a selected sample of those present on a particular farm. The intensity and direction of selection would have varied, however, depending upon the numbers available and the breeders ideas as to which pigs would make creditable records. These features of the data will be considered in greater detail later.

B. Adjustments

The effect of the particular pen in which an entry was housed was studied by Sutherland (1958) using the data from the first two seasons when each entry was housed in two pens. The components of variance ascribed to pens for daily gain and for probe constituted less than one

per cent of the total variance. This fact led to the conclusion that pen differences were unimportant and to the decision to house each entry in a single pen in the last three tests. The effect of pens will be ignored in this study.

A slightly different method of calculating daily gain was used in the last two seasons than in the first three seasons. During the first three seasons the number of days on test was taken as the number of days from the time the entry went on test to the time the pen averaged 200 pounds and was taken off test. The daily gain for each pig was calculated by dividing his total gain over the test period by the total days the pen was on test. The method allowed considerable variation in final weight for individuals in the pen. During the last two seasons the gain and the days on test were calculated from the beginning of the test to the date the individual pig was probed at about 200 pounds. This was done in order to measure gain more nearly over a weight-constant range. Since probing is done at 200 pounds little difference existed between the two measures. Presumably, the variability in gain would be greater under the first system than in the second. However, no significant heterogeneity of variance was evident between the two systems of calculating gain. The effect of any average difference between the two methods was confounded with seasons. All analyses were carried out within seasons. In view of these facts, no correction was made for the two methods.

The possibility and appropriateness of combining the information provided by the 467 barrows with that from the boars was considered.

Since the data from the boars were sufficient in most instances to give reasonable estimates, the risk of biasing these estimates with sex differences by including the barrow information did not seem justified. However, in the phase of the study where the variance of individual comparisons within pens were considered all the available data were needed to give stability to the estimates. An investigation into the nature and extent of the effects of sex on the traits under consideration was made in order to adjust the data for use in this later analysis.

The means of the two traits for each sex are given in Table 1. The means indicate little difference between the sexes for average daily gain while the barrows probe substantially higher than the boars. To investigate further the effects of sex on these two traits an analysis of variance was carried out.

Table 1. Mean daily gain and probe for boars and barrows

	Number	Gain	Probe
Boars	1266	1.84	1.25
Barrows	467	1.83	1.48

The model assumed for this analysis was:

$$y_{ijkl} = u + c_i + b_j + (cb)_{ij} + s_k + (cs)_{ik} + (bs)_{jk} + (cbs)_{ijk} + e_{ijkl} .$$

The observation, y_{ijkl}, is a linear function of the i-th seasons, the j-th breed and the k-th sex plus the interactions between these main effects. To evaluate the contribution of the main effects and of the interactions,

the mean squares were equated to their expectations and the resulting equations solved for the components of variance. The assumption that the main effects are uncorrelated is necessary to employ this method. This assumption is probably least appropriate in the case of breeds and seasons since the relative proportion of the breeds has changed over the five seasons. This will be considered in more detail in later analyses. The correlation between the constants later calculated for breed and sex in order to adjust the data was found to be essentially zero. The results of the analysis of variance are given in Table 2.

The effects of breeds and seasons are important sources of variation and will be discussed in detail in later analyses. The influence of sex appears negligible for daily gain but is more important than the other two factors for live probe. The interaction of sex with breed for probe contributes over two per cent of the total variance. The deposition of fat must be directly or indirectly under the influence of sex factors. The differential response of barrows and gilts has received considerable attention in the past and this sex difference has been found to contribute substantially to the variation in many characters but especially in carcass characteristics such as backfat thickness (Fredeen, 1953).

The breed by sex interaction may arise through breed differences in age and weight at sexual maturity. Warnick, et al. (1951) have investigated such differences and found significant differences between five inbred lines in age and in weight of gilts at puberty. Differences in sexual maturity are more difficult to measure between boars than

Table 2. Mean squares and components of variance from the analysis of the influence of sex on daily gain and probe

Source	d.f.	M.S.	Components of variance	
			Actual	Per cent
		Daily Gain		
Seasons	4	1.4950	.0038	8.3
Breeds	8	.5139	.0022	4.8
Seasons by breed	32	.1112	.0019	4.2
Sex	I	.0223	.0001	0.2
Seasons by sex	4	.0620	.0001	0.2
Breeds by sex	8	.0927	-.0004	-
Seasons by breeds by sex	32	.0293	.0006	1.3
Remainder	1643	.0370		81.0
		Probe		
Seasons	4	6.7481	.0177	18.4
Breed	8	2.2406	.0139	14.5
Seasons by breed	32	.1426	-.0063	-
Sex	I	17.8834	.0274	28.6
Seasons by sex	4	.7267	-.0056	-
Breed by sex	8	.0579	.0023	2.4
Season by breed by sex	32	.0426	.0034	3.5
Remainder	1643	.0312		32.5

between gilts but such differences probably exist, at least between breeds. Further possible influences on the differences between boars and barrows, which can not be evaluated in the present data, are the effects of selection by the breeders when deciding which individuals are castrated.

Considering the above variance analysis, the need for additional data, and the influence that selection may possibly have exerted, the following use was made of the information on the barrows. Least squares estimates of the sex effects for each breed separately were obtained from the data on the last three seasons. These constants were used to adjust the barrow data in the first two seasons. This barrow information from the two 1956 seasons, adjusted to a boar basis, was used in the analysis where the variances of individual comparisons within pens were studied.

IV. METHODS OF ANALYSIS

A. Analyses of Variance

The analysis of individual daily gains and live probes was carried out to determine the importance of genetic and environmental factors influencing these traits. Components of variance were estimated in the usual manner of equating the mean squares to their expectations and solving the resulting equations. To obtain components of covariance an analysis of the sum of gain and probe was carried out in addition to the analysis of each trait separately. Using the components of variance from the three separate analyses the components of covariance were obtained from the equation:

$$\text{Cov (Gain, Probe)} = \frac{1}{2}\left[\text{Var (Gain plus Probe)} - \text{Var(Gain)} - \text{Var(Probe)}\right] .$$

These procedures yield the same results as an analysis of covariance where sums of products are obtained. They were used here merely for convenience.

1. General analysis

The model used in the first general analysis of all boar data was as follows:

$$y_{ijklm} = u + c_i + b_j + (bc)_{ij} + s_{ijk} + d_{ijkl} + e_{ijklm} .$$

The y_{ijklm} is the observation on the m-th individual from the l-th dam within the k-th sire within the j-th breed and i-th season subclass. The components will be designated by capital letters corresponding to

small letters used in the model. A brief description of the content of the components will be given here and a fuller discussion presented later.

Components of variance associated with particular effects can be conveniently considered in terms of covariance. All the factors of a given classification which give rise to covariation among the individuals in that classification above the general level in the population contribute to the variance component associated with that effect.

The component for seasons, C, is composed of factors tending to make the individuals in a season more alike than random individuals in the population.

The components for breeds, B, represents the general covariance between individuals in a breed.

The component for the interaction of breeds and seasons, CB, measures the covariance between individuals in a particular breed and season after the average breed and season influence have been removed.

The separation and definitions of components described above is valid only under the conditions that the effects of breeds and seasons are not correlated. While there is no reason to suspect an inherent correlation between breeds and seasons the non-orthogonality of the data may produce a correlation between these factors. The correlation would arise if the proportions of the various breeds was not the same in each season. If the assumption of independence in the main effects of breeds and seasons is not valid then covariance terms between breeds and seasons appear in the expectations of the mean

squares. The influence that such a correlation has on the estimates obtained will be discussed later.

The remaining components may be described most accurately in terms of environmental effects and components of total genetic variance. The notation and concepts used in this study for the division of the total genetic variance are in the form developed by Malecot in terms of probability. The concepts are essentially the same as those first given by Wright in 1921 in terms of correlations between relatives. The form and symbolism vary slightly from that used by Wright and are given in detail by Kempthorne (1957).

The symbols σ^2_A and σ^2_D represent the additive and dominance portions of the total genetic variance. Components of epistatic variance are represented by combinations of the letters A and D, for example, σ^2_{AD}, signifying the interaction between the additive effect at one locus with the dominance effect at the second locus.

The symbol, f_{xy}, represents precisely one half the numerator of Wright's coefficient of relationship and is called by Malecot the "coefficient de parente". Malecot describes it in terms of probability as the probability that a random gene at a locus of individual x and a random gene from the same locus in the individual y are identical by descent. The probability that both genes at a locus in x are identical by descent with the two genes at that locus in y is given by u_{xy} which is equivalent to Wright's correlation between dominance deviations of two relatives.

The component, S, for sires contains all the influences which tend to make the individuals within groups by the same sire more alike than random members of the same breed-season group by different sires. The component, D, for dams in sire groups contains the genetic and environmental factors which are alike for full sibs but may differ for other paternal sibs. The direct maternal influence of the dam is included in this component as well as possible covariances between the maternal and genetic effects.

The expectations of the genetic portions of these components in a random mating population where there is no relationship among the dams mated to a particular sire is well known. All sire groups in this study where complete pedigree information back to the grandparents was available were used to calculate the average relationship in these data. The average value of f_{xy} in the sire groups of this study was found to be 0.155. Twice this value or, 0.31, is exactly the numerator of Wright's coefficient of relationship and corresponds to the situation where the dams mated to a particular sire are related only slightly less than half sisters. The value is almost identical to that found by Johansson and Korkman (1950) in Sweden. The expectation of the genetic portion of the sire and dam components using the value of 0.155 for f_{xy} are given below:

Covariance of Paternal Sibs, S, equals

$$.31\sigma^2_A + .06\sigma^2_D + \sum_{1<r+s\leq N} (.31)^R(.06)^S\sigma^2_{A^r D^s}$$

Covariance of Full Sibs minus the Covariance of Paternal Sibs, D, equals

$$.19\sigma^2_A + .19\sigma^2_D + \sum_{1<r+s\leq N} (.5)^R(.25)^S - (.31)^R(.06)^S \quad \sigma^2_{A^r D^s} \quad .$$

These expectations will be used throughout this study.

The residual variance, E, contains the remaining environmental variance and a genetic fraction equal to the total genetic variance less the covariance between full sibs.

One of the major difficulties in this study arises from the fact that the effect of farms is confounded with the effect of sires. This is the result of each farm sending one paternal half sib group to the testing station in a season. To estimate the genetic portion of the sire component some way must be found to remove the environmental fraction of this component. The following analyses were carried out for this purpose.

2. Analysis of farm effects

In the original model the component for sires was completely confounded with the effects of farms. However, some farms tested pigs in two or more seasons which allowed a modification of the original model to appraise the influence of farms. In general, the sires used on a single farm in two or more seasons were different. All farms were included in this analysis whether the sire changed from season to season or not. A further analysis of the small group of sires used in two consecutive seasons will be presented later. The effect of sires, s_{ijk}, was replaced by f_{jk} plus $(cf)_{ijk}$ to indicate the k-th farm in the j-th breed and the joint effect of the i-th season and the k-th farm.

With the same data the sum of the variance components CF and F will be equal to S. This analysis provides an estimate of that portion of the pre-test farm influences which is constant over several seasons. The component, CF, measures the genetic differences between sires on the same farm and the environmental influences peculiar to a given farm and season. Changes in the composition of the sow herd will be included within interaction as well as seasonal disease outbreaks and other factors not constant over seasons.

3. Analysis of the interaction of farms and seasons

The analysis of the average farm influence provided a measure of that portion of the farm environment which was constant over seasons. To determine the extent of farm influences which were peculiar to a particular season a further analysis was carried out. Included in this analysis were all farms which tested the offspring of a single sire in two consecutive seasons. The information from 287 individuals by 46 sires was included. Several modifications in the original model were necessary. The data divided logically into four groups of sires. The first season the sire appeared determined its group. Thus, there were four groups of sires, those appearing first in spring 1956, fall 1956, spring 1957 and fall 1957. The analysis was carried out within these groups and within breeds. The observation within breeds and groups, y_{ijk}, was represented by the following model:

$$y_{ijk} = u + c_i + s_j + (cs)_{ij} + e_{ijk} .$$

The model represents the trait of the k-th individual by the j-th sire in the i-th season within a given breed and group. The data were not sufficient to warrant estimating a dam component or a farm component. The sire component in this analysis will again contain the average farm influence.

The component for the interaction of sires and seasons will measure the extent of environmental interactions between farms and seasons, changes in the sow herd and genetic interactions of sires and seasons.

4. Estimation of heritability and genetic correlation

The components of variance provided by these variance analyses provided a means of estimating heritability and genetic correlations in these data. Heritability was estimated from the sire and dam components of variance and these values lie somewhere between the broad and narrow definition of heritability, Lush (1945). The sire and dam components free of all non-additive genetic variance and environmental confounding may be used to estimate heritability in the narrow sense by the following:

$$\frac{(1/2f_{xy})\,S}{S + D + E} \qquad \frac{2(S + D)}{S + D + E} \quad .$$

If the differences between the sire and dam components were only the result of dominance deviations and maternal influences then the two measures of heritability could provide some insight into the size of this contribution. The expectations of S and D given previously showed that these components contain various fractions of dominance and epistatic

variance. Since environmental contributions and sampling errors further obscure the picture, estimation of the additive genetic variance and maternal influences is seldom straight forward.

Under the same assumptions that were used to estimate heritability, the components may be used to estimate genetic correlation. Letting the sire component of variance for gain and probe be S_G and S_P, respectively, and the sire component of covariance, S_{GP}, then the genetic correlation is given by:

$$r_{g_G g_P} = \frac{S_{GP}}{\sqrt{S_G \cdot S_P}} \quad .$$

Any biases in the components of variance and covariance will influence this correlation. Although environmental correlations are probably the most important source of error in estimating these genetic correlations, sampling errors are also known to be high, especially when the sire components are small.

B. Analysis of Specific Relationships

The analyses of variance given previously are designed mainly to separate the two major influences, that of the genotype and that of the environment. The following investigation was carried out to determine the importance of various fractions of the genetic variance and covariance and the extent of maternal influences in daily gain and probe.

The regulations of the testing station required the individuals within an entry to be at least half sibs. However, the degree of relationship

between the pigs in an entry varied from as little as that between merely paternal half sibs to that between full sibs depending on the relationship among the dams. Here and throughout this study it is assumed that there is no relationship between the sire and the dam to which he is mated; that is, that there is no inbreeding. This assumption is approximately true, as breeders very rarely inbreed. This variability in degree of relationship gave some opportunity to assess various components of genetic variance.

The identity of the grandparents of the individual pigs was available in most instances. With this information the relationship between the pigs within each pen was calculated. The first two seasons the pen of three pigs consisted of a barrow and two boars. The barrow was corrected to a boar basis as noted previously. The three boars in each entry during the last three seasons provided the remaining data for this analysis. There were two pens of related individuals in the first two seasons but the relationships between pens were not used. When the size of the entry was six pigs the regulations requiring the pigs to be from at least three dams allowed some pens of full sibs. This could occur only in the first two seasons and was not possible later when the entry was reduced to four individuals.

The pens were classified according to the type of relationship existing among the dams of the individuals in the pen. These classes, grouped according to the number of separate dams appearing in the pedigrees of the three individuals in a pen are listed below.

(a) Three dams

Class 1. All dams unrelated

Class 2. All dams half sibs

Class 3. All dams full sibs

Class 4. Two dams half sibs and one unrelated

Class 5. Two dams full sibs and one half sib

Class 6. Two dams full sibs and one unrelated

(b) Two dams

Class 7. Dams half sibs

Class 8. Dams full sibs

Class 9. Dams unrelated

(c) One dam

Class 10. Dam the same for each individual.

In a pen of three pigs there are two independent or orthogonal comparisons between the individual pigs. The expected values of these comparisons may be written in terms of the components of genetic variance or covariance if the relationships are known. The general form of the genetic covariance between individuals X and Y is:

$$\mathrm{Cov}(X, Y) = 2f_{xy}\sigma^2_A + u_{xy}\sigma^2_D + \sum_{1<R+S\leq N} (2f_{xy})^R (u_{xy})^S \sigma^2_{A^r D^s} \quad .$$

The summation is over the n loci contributing to the trait. The values of the genetic covariance are given in Table 3 for the case where the individuals have a common sire but different degrees of relationship exist between their dams. From this table it is possible to write the expectations of any comparison within the ten classes of pens in terms

Table 3. The genetic covariance between individuals with a common sire and various relationships existing among the dams

Relationship of dams	Coefficients of the variance components				
	σ^2_A	σ^2_D	σ^2_{AA}	...	σ^2_M
Dams unrelated (Cov Q)	1/4	0	1/16		0
Dams half sibs (Cov R)	5/16	1/16	25/256		0
Dams full sibs (Cov S)	3/8	1/8	9/64		0
The same dam (Cov T)	1/2	1/4	1/4		1

of genetic, maternal and environmental parameters.

Let the expression of a trait in an individual, I, be written as the sum of environmental (E), genetic (G), and maternal (M) effects where these are expressed as deviations from a pen mean, as follows:

$$I = E + G + M .$$

The genetic portion will include the additive, dominance and epistatic components. The following definitions are used:

$$E(I^2) = V(E) + V(G) + V(M)$$

$$E(II') = Cov(EE') + Cov(GG') + Cov(MM') .$$

The total phenotypic variance on a within pen basis is given by:

$$V(P) = V(E) + V(G) + V(M) .$$

The expected value of any comparison between individuals in a pen can be written in terms of these definitions. Thus, for individual X and Y,

the following comparison can be made:

$$E\ \frac{1}{2}(X-Y)^2 = V(P) - Cov(X, Y) .$$

The Cov(X, Y) is the sum of the genetic and maternal covariances between X and Y and will depend on the relationship between the two individuals as shown in Table 3.

For example, let X, Y and Z represent three paternal sibs in a pen. Furthermore, let the dams of X and Y be full sibs while the dam of Z is unrelated to either of the other dams. This is an example of relationships as described in Class 6. Two independent or orthogonal comparisons have the following expectations:

$$E\ \frac{1}{2}(X-Y)^2 = V(P) - Cov(S)$$

$$E\ \frac{1}{6}(X+Y-2Z)^2 = V(P) + (1/3)\ Cov(S) - (4/3)\ Cov\ (Q) .$$

The covariance between two traits can be written and studied in an analogous manner. The algebraic sum of the two traits is used as the observation on each individual. Designating the two traits with subscripts 1 and 2, the following comparison of individuals X and Y is used:

$$E\ \frac{1}{2}\left[(X_1+X_2) - (Y_1+Y_2)\right]^2 - E\ \frac{1}{2}(X_1-Y_1)^2 - E\ \frac{1}{2}(X_2-Y_2)^2$$

$$= 2E(X_1X_2 + Y_1Y_2 - X_1Y_2 - X_2Y_1) .$$

The sum of genetic, maternal and environmental covariance between traits one and two in the same individual plus the environmental covariance between traits one and two in different individuals in a pen can be considered as the total phenotypic covariance within pens in the same

manner as the total intra-pen phenotypic variance was defined. Thus one-half of the expectation given above is equal to the following:

$$\text{Cov}(P_1P_2) - \text{Cov}(X_1Y_2) \ .$$

The phenotypic covariance, Cov P_1P_2, between two traits is defined above and the $\text{Cov}(X_1Y_2)$ has the same expectation as Cov(X, Y) in Table 3 except that the components of genetic and maternal variance are replaced by components of genetic and maternal covariance. If, for example, X and Y are related as paternal sibs from full sib dams, then the comparison given above is equal to the following expression:

$$\text{Cov}(P_1P_2) - 3/8\ \text{Cov}A_1A_2 - 1/8\ \text{Cov}\ D_1D_2 - \ldots - 0\ \text{Cov}\ M_1M_2$$

where Cov A_1A_2 = genetic covariance of additive deviations

Cov D_1D_2 = genetic covariance of dominance deviations

Cov M_1M_2 = covariance of maternal influences.

Two orthogonal comparisons were made within each pen on daily gain and backfat probe and on the sum of these two traits. These comparisons were then grouped into ten distinct types and these are listed in Table 4 with the number of observations on each type.

The observed comparisons equated to their expectations give a set of observations which are linear functions of the known constants and unknown parameters. The method of least squares gives unbiased estimates of these parameters if the assumptions of uncorrelated and homogeneous errors are appropriate.

Some of the assumptions made in these estimating procedures deserve emphasis. The model describing the phenotype as a linear

Table 4. Types of variance and covariance estimated by individual pen comparisons with a single degree of freedom

Type	No. Obs.	Coefficients of Components of Variance				
		σ^2_E *	σ^2_A	σ^2_D	σ^2_{AA} ...	σ^2_M
1	42	1.0	.7500	1.0000	.9531	1.3333
2	207	1.0	.7500	1.0000	.9575	1.0000
3	25	1.0	.7083	.9583	.9167	1.0000
4	87	1.0	.6875	.9375	.9023	1.0000
5	8	1.0	.6667	.9167	.8958	1.3333
6	49	1.0	.7708	1.0208	.9492	1.0000
7	66	1.0	.6250	.8750	.8594	1.0000
8	89	1.0	.5833	.8333	.8125	0.3333
9	88	1.0	.5000	.7500	.7500	0.0000
10	23	1.0	.7917	1.0417	.9635	1.0000

* $\sigma^2_E = V(E) - Cov(E\ E')$.

combination of the genetic and environmental effects may not be valid. If any of the components of the genotype interact with the environment then a joint term of genetic-environmental interaction should be included in the model.

The only consideration of maternal effects in this model is that of the direct influence of the dam. A more complete model would include the covariances between the maternal influence of the dam and her genotype. For further account of this see Kempthorne (1957). Dickerson and Grimes (1947), for example, suggested that there may be a negative relationship between good milking ability and genetic factors for

economy of gain.

The expectation of the genetic parameters in Table 4 point out the restricted range over which the coefficients vary in this study. All the individuals in a pen are paternal-sibs. Therefore, the coefficient of the additive component is forced to be less than one. Furthermore, without inbreeding, this coefficient can not be less than one half. The coefficient for the other components vary over an even more restricted range. This limited range of coefficients reduces the reliability of the parameter estimates. The structure of the data is such that the coefficients of the additive and dominance components of variance are linearly dependent and,therefore, only a joint estimation of these terms is possible. The basis of this dependency can be demonstrated from the definitions of f_{xy} and u_{xy} in terms of probabilities of genes being identical by descent. Let p_1 equal the probability that the genes which individuals X and Y receive from their sire at a particular locus are identical by descent and p_2 equal the probability that the genes they receive at this locus from their dams are identical by descent. Then f_{xy} is defined as $\frac{1}{2}(p_1+p_2)$ and u_{xy} as p_1p_2. In the present data all individuals in any related group have a common sire and, therefore, the probability of the genes they receive from the sire being identical by descent is constant and equal to one half. It is then easily shown that $f_{xy} = 1/4 + (1/4)p_2$ and $u_{xy} = (1/4)p_2$ or $u_{xy} = f_{xy} - 1/4$. Thus all the coefficients of the components of genetic variance in the present study can be expressed in terms of f_{xy} or one half the numerator of Wright's coefficient of relationship. The fact should be

emphasized that the resulting relationships between these coefficients do not hold in all population but are found here as a very special case arising from the structure of the related groups.

The genetic covariances obtained from the analysis of variance were shown to contain varying amounts of epistatic components. The same situation will arise in estimating the genetic variance by the methods described here. The joint estimate of the additive and dominance variance when components of epistatic variance are ignored in the model will contain fractions of the epistatic variance in so far as the coefficients of these epistatic components are related linearly to the coefficient of the additive component.

V. RESULTS AND DISCUSSION

A. Breed and Season Means

The average daily gain and probe for each breed are presented in Table 5. These means suggest marked breed differences, especially in probe. The six breeds, Duroc, Hampshire, Landrace, Poland China, Spotted Poland China and Yorkshire, which make up almost ninety per cent of the data, generally contain the faster gaining and lower probing animals. Similar unweighted means for each season are given in Table 5. The decline in probe from 1956 to 1958 is impressive. A similar but less drastic downward trend in gain occurred.

Table 5. Breed and season means for average daily gain and backfat probe

Breed	No. Obs.	Mean Daily Gain	Mean Probe
Berkshire	41	1.72	1.22
Chester White	63	1.75	1.51
Duroc	244	1.90	1.35
Hampshire	316	1.84	1.19
Landrace	143	1.87	1.15
Poland China	203	1.80	1.24
Spotted Poland	107	1.84	1.23
Tamworth	30	1.78	1.44
Yorkshire	119	1.84	1.17
Season			
Spring 1956	186	1.89	1.46
Fall 1956	202	1.96	1.31
Spring 1957	284	1.82	1.25
Fall 1957	291	1.79	1.11
Spring 1958	303	1.80	1.21

B. Analyses of Variance

1. General analysis

The results from the general analysis of variance are presented in Table 6. The expectations of the mean squares given in Table 7 show the extent of non-orthogonality in the data. The components of variance for each effect are given in Table 8 together with the percentage of the total variance each represents. Estimates of heritability and correlation obtained from the analysis are also given in Table 8.

The variance components for daily gain indicate that season differences contribute over nine per cent of the total variance and breeds over three per cent of the total variance. The interaction between breeds and seasons contributes almost as much to the total variance as breeds. The reason for such an interaction is not immediately clear and a further investigation of this aspect of the data was made.

Table 6. General analysis of variance for daily gain and probe

Source	D.F.	Mean Squares		
		Gain	Probe	Gain + Probe
Seasons	4	1.2070	3.6313	7.6812
Breeds	8	0.3258	1.4228	1.5271
Seasons by breeds	32	0.0874	-0.0549	0.0284
Within breed-season groups				
Sires	350	0.0529	0.0529	0.1379
Dams in sires	673	0.0310	0.0219	0.0658
Full sibs in dams in sires	198	0.0290	0.0130	0.0481

Table 7. Expectations of mean squares in the general analysis of variance

Source	Coefficients of Components of Variance					
	E	D	S	CB	B	C
Seasons	1.000	1.371	3.406	42.200	3.410	250.832
Breeds	1.000	1.359	3.348	30.093	133.249	2.865
Seasons by breeds	1.000	1.401	3.387	25.363	-0.426	-0.716
Within breed-season groups						
Sires	1.000	1.284	3.183			
Dams in sires	1.000	1.120				
Full sibs in dams in sires	1.000					

Table 8. Components of variance and covariance, heritabilities, phenotypic and genetic correlations from the general analysis of variance

Source	Components of Variance and Covariance				
	Gain		Probe		Gain and Probe
	Actual	Percent	Actual	Percent	Actual
Season	.0043	9.6	.0147	26.3	.0058
Breed	.0016	3.6	.0108	19.4	-.0009
Season by breed	.0014	3.1	-.0038	--	.0018
Sires	.0068	15.1	.0094	16.8	.0028
Dams	.0018	4.0	.0079	14.2	.0030
Full sibs	.0290	64.6	.0130	23.3	.0030

Heritability of differences within breed and season groups

	Gain	Probe
$\frac{(\frac{1}{.31})S}{S + D + E}$	0.58	1.00
$\frac{2(S + D)}{S + D + E}$	0.46	1.14

Correlation between Gain and Probe

Phenotypic	0.26
Genetic	0.35

First, it was pointed out previously that the method of obtaining the components of variance by equating the mean squares to their expectations rests on the assump tion that the main effects, breeds and seasons in the present case, are uncorrelated. There is no reason to suspect an inherent correlation between these two factors and if the data were orthogonal the assumption of independence would undoubtedly hold. However, non-orthogonality which arises from an unequal distribution of the breeds over the seasons confounds breed and season effects and may result in a correlation between the effects of breed and the effect of seasons. To investigate the possible biases resulting from this correlation, the values of the constants for breeds and seasons were obtained by least squares. The correlation between these constants would, of course, be zero if the data were orthogonal. In the present instance this correlation was -0.13 for daily gain and zero for probe. The assumption of independence of the main effects must, therefore, be questioned in daily gain. The result of a negative covariance between breeds and seasons is to bias the estimates of the main effects downward and inflate the estimate of the interaction. The components for Seasons, Breeds and Breed by Seasons were .0043, .0016 and .0014, respectively, as they appear in Table 8. Adjusting these for the correlation between breeds and seasons they become .0048, .0021 and .0009 which are not greatly different than those obtained before but which does show that the interaction is less important than it first appears.

To investigate this interaction further an analysis was carried out to determine whether the breeds react in a differential manner to the fall and spring testing. The extreme difference in climate between hot summer months and cold winter period might be expected to have a differential effect on the fatter and leaner breeds. The data failed to show any general difference in daily gain or probe between fall and spring testing. Furthermore, the interaction of breeds could not be ascribed to the general effects of fall and spring testing. The explanation for the breed by season interaction based on the assumption of differential breed response to summer and winter climate was not supported by the data.

The daily gain declined from 1956 testing seasons to the 1957 and 1958 testing seasons. The sum of squares for seasons was divided into a single degree of freedom representing the differences between these two periods and the remaining three degrees of freedom for differences among seasons in these groups. Corresponding interaction sums of squares were obtained for breeds with these two periods and for breeds by seasons within these periods. The results are shown in Table 9.

The results presented in Table 9 clearly show the major part of the season differences are associated with differences between the first two tests and the last three tests; that is, with a general time trend. Furthermore, the interaction of breeds and seasons is largely the result of a differential general time trend in the breeds.

Table 9. Partition of breed and season sums of squares from the general analysis of daily gains

Source	D.F.	S.S.	M.S.
Seasons (4)			
1956 vs. 1957-58 time trend	1	4.1316	4.1316
Within time periods	3	0.6965	0.2321
Breeds (8)			
Seasons by breeds (32)			
Time trend by breed	8	1.6837	0.2105
Within time periods by breeds	24	1.1116	0.0463

The reasons behind such a differential time trend in the breeds are not completely clear. The partitioning of the season sum of squares into the comparison of 1956 with 1957 and 1958 corresponds exactly with the subdivision into the two types of testing procedures. In 1956, the pigs from a breeder were fed in two pens with three pigs per pen while in the remaining seasons an entry of four pigs was fed in a single pen. It is not possible to determine whether the decline in gain is the result of crowding in the pen or is a response correlated with the decline in probe or has some other explanation. There is some evidence for competition effects in swine (Jonsson, 1957). It is at least remotely possible that certain breeds can meet the stress of four pigs to a pen more satisfactorily than other breeds and thus suffer less decline in gain. However, the difference in competition within three pig and four pig pens seems unlikely to have been large.

The components within breed and season groups would provide estimates of the genetic parameters in the population if they were free of effects of common environment for pigs in the same test group. The sire component for daily gain, representing fifteen per cent of the total variance, yields heritability figures far in excess of previous estimates. Environmental effects persisting from the home farm and causing the individuals in an entry to be more alike than is expected on the basis of their genetic make-up are almost surely present. The estimate of heritability provided by the combination of components for dams and sires is more reasonable although still high. This estimate is not inflated by farm or farm by season influences to as large an extent but, of course, contains in its expectations more of any non-additive genetic variance plus all the direct maternal influence. Almost sixty-five per cent of the total variance in daily gain or seventy-seven per cent of the variance within breed and season groups remains within litters after the above sources have been removed.

The analysis concerning probe presents a different picture from that of daily gain. The probe means had declined sharply over the period studied and the analysis shows that this was a larger part of the total. Seasons represent over twenty-six per cent of the total variance. Larger breed differences exist in probe than in gain. The season by breed interaction yielded a negative component of variance which, if season and breed effects were uncorrelated, could be an estimate close to zero. Actually, the correlation between the breed and season constants was calculated and found to be essentially zero. The sire

component in the analysis of probe also appears to be carrying a large portion of environmental influences in addition to its genetic expectations. Both the sire and the dam component yield estimates of heritability of intra-breed and season differences in excess of one. This indicates the difficulties which result from supposing that these components are clean estimates of additive genetic variance. Presumably the major trouble is the inclusion of some intra-breed farm differences. These could be either of environmental or genetic origin. The inflation of the dam component can not be attributed to farm differences since it measures only the differences between dams on the same farm. It seems unlikely that all this is due to direct maternal influences although differences between sows in milking ability may have made the litters differ markedly at weaning.

The components of covariance provide a means of estimating genetic and phenotypic correlations which were found to be 0.35 and 0.26, respectively. To consider that components of covariance attributed to the sires are estimates of genetic parameters assumes that they arise only from a covariance between the additive genetic effects among the paternal sibs. In the present study an environmental correlation between members of the paternal sib groups is surely present. This correlation arises from the fact that the paternal sibs are raised on the same farm and tested in the same pen. In general, the factors which tend to make an individual grow faster would also tend to make that individual fatter. Thus, environmental factors are probably tending to increase the sire component of covariance, although unlike variance components, it is possible that

environmental confounding might reduce the covariance component. Since both the sire components of variances and covariances are probably biased upward in this study it is hard to determine just how the estimate of genetic correlation is affected, although it also appears to be too large. That the phenotypic and genetic correlations are positive helps to explain why the decline in probe has been accompanied by a similar, but smaller, decline in daily gain.

This preliminary or general analysis of the data serves to define and emphasize the direction in which further study is needed. First, the sire components appear to contain a considerable portion of non-genetic variance. This must be removed before a dependable estimate of the additive variance is possible. Secondly, in the analysis of probe the dam component is larger than seems reasonable, even under a model allowing for maternal effects and dominance. Finally, even after these influences have been explained, there remains the task of dividing the genetic variance into its components. This latter problem will be attacked by using the information available on the relationship between individual animals.

2. Analysis of farm effects

The average effect of farms was estimated by splitting the sire component from the general analysis into two parts. The components were called farm and farm by season components and their estimation was possible from the fact that 206 farms had entered pigs in more than one testing season. This group included entries by the same and different sires although the number of sires used in two seasons was only forty-six.

The values of the components for Seasons, Breeds, Breed by Seasons, Dams and Full Sibs in Dams should be the same in this analysis as they were in the general analysis since the same data were used. The components are obtained from the solution of a set of equations and rounding errors prevent exact equality in the two analyses. The sum of the farm and farm by season components will be equal to the sire component from the general analysis. (Table 8)

The mean squares are presented in Table 10 and their expectations in Table 11. The values of particular variance components are given in Table 12 with the per cent of the variance accounted for by each. Components of covariance are also given here. The farm by season component is equivalent to the sire component with the average effects

Table 10. Analysis of variance for daily gain and probe to estimate the influence of farms

Source	d.f.	Mean Squares		
		Gain	Probe	Gain plus Probe
Within Breeds				
Farms	197	.0607	.0902	.1998
Seasons by farms (Sires)	153	.0429	.0049	.0581
Dams in Season x farm	673	.0310	.0219	.0658
Full sibs in Dams	198	.0290	.0130	.0481

Table 11. Expectation of mean squares in Table 10

Source	Coefficients of components of variance					
	E	D	CF	F	CB	C
Within breeds						
Farms	1.000	1.286	3.187	6.063	1.890	1.890
Seasons by farms (Sires)	1.000	1.286	3.177	-0.526	-2.433	-2.433
Dams in season by farm	1.000	1.120				
Full sibs in dams	1.000					

of farms removed. This would allow its use in estimation of heritability and correlation as is given in Table 12 if it contained no environmental contribution. However, some environmental influences may still be present in the farm by season interaction.

Daily gain appears to be little influenced by the average pre-test environment of the farm. The conditions of the farm which are not constant over seasons may still be contributing substantially to the sire component.

Probe, unlike daily gain, appears to be strongly influenced by differences between farms. The component for farms represents ten per cent of the total variance. The nature of these differences between farms can not be ascertained from these data but it is reasonable to assume they are both environmental and genetic. All influences, peculiar to a farm and constant over seasons, which affect the final

Table 12. Components of variance and covariance, heritabilities, phenotypic and genetic correlation from the analysis to estimate the influence of farms

Source	Components of variance and covariance				
	Gain		Probe		Gain and probe
	Actual	Percent	Actual	Percent	
Seasons, breeds and seasons by breeds		16.0		45.5	
Farms	-.0011	-	.0056	10.1	-.0004
Seasons by farms	.0078	17.0	.0038	6.8	.0032
Dams	.0018	3.9	.0079	14.2	.0030
Full sibs	.0290	63.0	.0130	23.4	.0030

Heritability of intra-breed and season differences

	Gain	Probe
$\frac{\frac{1}{.31}(CF)}{CF + D + E}$	0.65	0.49
$\frac{2(CF + D)}{CF + D + E}$	0.50	0.95

Correlation between gain and probe

Phenotypic	0.28
Genetic	0.59

probe are contained in this farm component. The emphasis on lean pigs is a relatively recent trend. The amount of selection for this trait has surely varied between farms. This would cause genetic differences between farms, and such differences would be included in the average farm effects.

The estimates of heritability for daily gain changed very little, since the farm influence was small. The heritability of probe, estimated from the sire component has been reduced to 0.49 which agrees reasonably well with previous reports in the literature.

The large reduction in the sire component of variance for probe coupled with a relatively unchanged sire component of covariance between gain and probe, has increased sharply the estimate of genetic correlation.

The present analysis serves mainly to explain and separate from the sire component for live probe the influences of farms which persist over two or more seasons. The separation of the farm effects from the sire component for probe gives a reasonable estimate of heritability. Still remaining to be determined are the causes for the high estimate for the farm by season component for daily gain.

3. Analysis of farm by season interactions

A further analysis was made of all sires used in two consecutive seasons to determine the extent of farm by season interaction. The analysis was done within groups and breeds as described previously and the mean squares are presented in Table 13. The expectations of the mean squares are given in Table 14. The components of variance and covariance from this analysis are given in Table 15 with estimates of heritability and correlation.

The numbers available for this analysis are small but the interaction of sires and seasons appears to be important. Representing five per cent of the variance in gain and ten per cent in probe this interaction

Table 13. Analysis of variance to estimate the influence of farm by season interactions

Source	d.f.	Mean squares		
		Gain	Probe	Gain plus probe
Within groups and breeds				
Seasons	19	.0793	.0473	.1871
Sires	27	.0491	.0726	.1802
Seasons x sires	27	.0429	.0289	.0906
Remainder	195	.0359	.0173	.0672

Table 14. Expectations of the mean squares in the analysis to estimate the influence of farm by season interactions

Source	Coefficients of components of variance			
	E	SC	S	C
Within groups and breeds				
Seasons	1.000	3.144	0.016	7.500
Sires	1.000	3.123	6.176	0.024
Seasons x sires	1.000	3.041	-0.012	-0.024
Remainder	1.000			

Table 15. Components of variance and covariance, heritability, phenotypic and genetic correlations from the analysis to estimate the influence of farm by season interaction

Source	Components of variance and covariance				
	Gain		Probe		Gain and Probe
	Actual	Percent	Actual	Percent	Actual
Within groups and breeds		5.0		20.4	
Seasons	.0048	10.4	.0024	6.3	.0028
Sires	.0009	1.9	.0069	18.0	.0032
Seasons by sires	.0023	5.0	.0039	10.2	.0008
Remainder	.0359	77.7	.0173	45.2	.0007

Heritability of intra-breed and group differences

$\frac{(\frac{I}{.31})S}{S + SC + E}$	Gain	Probe
	.07	.79

Correlation between gain and probe

Phenotypic	0.14
Genetic	1.28

warrants some consideration in the analysis of the data. The covariance components appear to be relatively unaffected by this interaction.

The causes of this interaction may be considered in two separate parts, environmental and genetic. Included in the environmental portion would be all factors associated with pre-test conditions during

the particular season but not constant over the two seasons on the same farm. Examples are such conditions as disease outbreaks, severe weather, or changes in feeding from one season to the next. Any of these factors which affect the final expression of the traits will result in a sire by season interaction.

This interaction may result from another environmental cause produced mainly by the regulations governing the testing. The average weight of an entry must be sixty pounds or less on arrival at the station. If the breeder wants to enter pigs that appear to be growing too fast to meet this requirement, he may possibly withhold feed from them for a short period before they are sent to the testing station. If this practice influences daily gain and probe and is done by some breeders in some seasons but not in others it would cause some interaction of sires and seasons.

The genetic portion of this component will arise from a change in the composition of the sow herd and possibly from the interaction of the sire genotype with the environment of a given season. The interactions of the genotype with the environment or season can not be separated from those of farm and seasons. Since the importance of genetic by environmental interaction in large animals is not well established, the possibility of such interaction can not be ruled out. Probably the major share of the sire by season interaction here arises from environmental effects of farms interacting over seasons.

The estimates of heritability computed from the results of this analysis are lower than any obtained in the previous analyses. The estimate for probe is still biased upward in the present analysis since no allowance for average farm differences was made. The components of covariance agree closely with those obtained previously and the covariance does not appear to be influenced by the farm by season interaction. The unchanged sire component of covariance and greatly reduced estimates of sire components of variance led to a genetic correlation of over one. The numbers in this analysis are small and sampling consequently high.

C. Evaluation of the Selective Nature of the Data

Pigs sent to the testing station are a selected group of animals and not a random sample of the animals from a given farm. The influence of this selection on the results in this study was considered.

The problem has two general aspects. First, how accurately and intensely does the individual breeder select for daily gain and probe at weaning? Secondly, how does such selection influence the estimates of components of variance in this study?

The accuracy of selection at weaning for final performance on test depends on the ability of the individual breeder to estimate the future performance of young pigs. The only available experimental data to measure this ability are scores placed on 162 individuals during one season by a single judge. As the entries arrived at the station or

within ten days thereafter, the judge placed a score on each pig using numbers four through twelve to rank them from predicted slow to fast gainers. In addition, he predicted the final probe in inches of backfat. The correlations between predicted and actual measures were 0.15 and 0.39 for daily gain and for probe, respectively. The over-all correlations were nearly the same as the intra-breed and intra-entry correlation and there was no evidence that the predictions were any different within these classifications. Clearly, this judge had some limited ability to evaluate individuals at weaning for final performance on test although the correlation between gain scores and actual gains is not highly significant. Nothing is known about the average ability of the breeders to do similar scoring. It is extremely hazardous to extrapolate the results of a single judge to the average ability of the breeders. It seems reasonable that some characteristics in individual pigs at weaning would allow an experienced man to predict their final performance with partial success. The unknowns which preclude the use of this single judge as typical of all breeders include the fact that he probably had considerably more training in livestock judging. However, each breeder can observe his pigs from birth and also has the benefit of information about their parents and collateral relatives.

The intensity of selection may be evaluated from several sources of data. A questionnaire returned by seventy-one breeders in one testing season was tabulated to find the average size of the swine herds and their general breeding procedures. The average breeder kept eighteen sows and used two boars each season. The number of litters

from which a particular breeder could select pigs for his entry is limited by the regulations of the station. These require that the pigs must come from at least three litters by the same sire. The number of pigs in each litter at birth must be eight for gilt and nine for sow litters. The available litters are further limited in that the sow must farrow at such a time that her pigs are of acceptable size during the period when the pigs are accepted for testing. All these factors combined with the fact that each entry must be from a single sire necessarily reduces the inter-litter selection that a breeder can practice.

To evaluate the effects of selection on the components of variance obtained in the previous analyses is difficult, especially since the evidence on the intensity and accuracy of selection is fragmentary and not precise in any manner. Presumbly, if selection has differed in intensity and direction between farms, the sire or farm component in the present analysis will reflect this effect and be larger than it would have been without selection. If selection were strong and in the same direction it could reduce the farm component. The effect of selection within farms is more difficult to predict. The dam component for probe was pointed out to be higher than could reasonably be expected on the basis of genetic and maternal influences. Types of selection which tend to increase the differences between dams or reduce differences between full sibs might be the cause of this apparent discrepancy but with the present data it is not possible to make more precise statements on the effects of such selection.

D. Analysis of Specific Relationships

The average values of the variance computed for specific relationships within pens are given in Table 16 for the possible types of comparisons listed in Table 4. The figures in this table demonstrate the large sampling fluctuations inherent in estimates of variance. No trends are evident, except in probe where the variance declines considerably with increasing relationship.

The first analyses carried out attempted to separate the environmental portion of the intra-pen variance from the joint value contributed by the additive and dominance components of genetic variance. Epistatic deviations and maternal effects were ignored. The estimates of these components for gain and probe and the covariance of these two traits are presented in Table 17. The standard errors of these estimates are large showing approximately how much confidence can be placed in the estimates.

The joint estimate of additive and dominance variance and the value of the environmental component for daily gain in Table 17 are in reasonable agreement with the previous reports on this trait. The genetic portion of the variance in gain, .0111, is considerably smaller than .0219, the estimate found by dividing the sire component in Table 8 by the average relationship within sire groups. This further confirms that the paternal sib covariances are probably biased upward through the effects of farm by season interactions. The heritability of gain constructed from this analysis by using the genetic component divided by the sum of the genetic and environmental

Table 16. The mean values of intra-pen variances and covariances listed in descending order of the coefficient of the additive component

Type of variance as listed in Table 4	Coefficient of the additive component	No. observations	Variance of gain	Variance of probe	Covariance of gain and probe
10	.7917	23	.0296	.0320	.0046
6	.7708	49	.0317	.0258	.0374
1	.7500	42	.0261	.0252	.0441
2	.7500	207	.0299	.0225	-.0001
3	.7083	25	.0158	.0206	.0239
4	.6875	87	.0318	.0230	.0068
5	.6667	8	.0300	.0158	.0144
7	.6250	66	.0361	.0182	.0023
8	.5833	89	.0348	.0182	.0487
9	.5000	88	.0209	.0139	.0001

Table 17. Least squares estimates of components of intra-pen variance from the analysis of relationships within pens

I. Model $\sigma^2_P = \sigma^2_E + \sigma^2_A + \sigma^2_D$			
Variance in daily gain:	σ^2_E	$\sigma^2_A + \sigma^2_D$	
Estimate	.0221	.0111	
S. E.	.0127	.0186	
Variance in probe:	σ^2_E	$\sigma^2_A + \sigma^2_D$	
Estimate	-.0060	.0400	
S. E.	.0100	.0143	
Covariance in gain and probe:	$\sigma_{E_1E_2}$	$\sigma_{A_1A_2} + \sigma_{D_1D_2}$	
Estimate	.0220	-.0119	
S. E.	.0184	.0271	
II. Model $\sigma^2_P = \sigma^2_E + \sigma^2_A + \sigma^2_D + \sigma^2_M$			
Variance in daily gain:	σ^2_E	$\sigma^2_A + \sigma^2_D$	σ^2_M
Estimate	.0341	-.0147	.0068
S. E.	.0205	.0394	.0091
Variance in probe:	σ^2_E	$\sigma^2_A + \sigma^2_D$	σ^2_M
Estimate	-.0089	.0462	-.0016
S. E.	.0158	.0303	.0022
Covariance in gain and probe:			
	$\sigma_{E_1E_2}$	$\sigma_{A_1A_2} + \sigma_{D_1D_2}$	$\sigma_{M_1M_2}$
Estimate	.0111	.0116	-.0062
S. E.	.0297	.0573	.0134

components was 0.33, which is lower than either estimate in Table 8 but more nearly agrees with previously reported values on this trait. Again there is support that environmental correlations were included in the sire component and inflated by the multiplication with the reciprocal of the relationship.

The results for probe can not be as readily reconciled with expectations as those for gain. The negative estimate of environmental variance is a logical contradiction and indicates deficiencies in the model or large sampling errors. As the relationship increases the average variance is reduced more than can be expected on the basis of the additive relationship. Although the results logically can be charged to the large sampling errors, this does not rule out other possible biases in the estimates.

The analysis of the covariance between gain and probe is also contradictory to the previous results. The estimate of genetic covariance is negative and the genetic correlation calculated from these estimates is -0.56.

The second model in Table 17 includes the influence of maternal effects and the analysis attempts to separate the genetic, environmental and maternal components in the variance within pens. The model is identical to that used in the first analysis except that maternal effects are included. The results are shown in the lower part of Table 17. The accuracy of the estimates declines rapidly as more parameters are included in the model, as is evident from the standard errors attached to the components. The addition of the maternal component does not

help to explain the apparent contradiction in the previous probe estimates. The environmental variance is still estimated as a negative quantity. Furthermore, the estimate of the additive plus dominance variance in gain has become negative under the model including maternal influences. The estimates of the covariance components between gain and probe follow the results presented in Table 8 much more closely under the present model where maternal effects are considered. Using this estimate of genetic covariance and the two estimates of genetic variance derived under the previous model the genetic correlation is 0.55. This value agrees substantially with others in this study, all of which are higher than most of the values previously reported for this genetic association.

The attempts to fit larger models including epistatic components were generally unsuccessful and gave contradictory solutions where solutions were possible. First, the correlations between the coefficients for the components became large and made the solutions of the normal equations difficult. These conditions further imposed tremendous sampling variances on the estimates. A wider range of relationships and a larger volume of data would improve this situation and reduce the errors in estimation.

E. Summary of the Estimates of Genetic and Environmental Parameters

Many separate analyses have been employed to resolve the genetic and environmental contributions to the variability in daily gain and probe. The following summary consolidates and reviews briefly the estimates obtained in these analyses. Table 18 gives the estimates of genetic variance obtained for daily gain and probe, together with the expectations of each estimate and the calculated heritability. The heritability of one-quarter for daily gain and one-half for live probe seems close to the general results of earlier work reported in the literature. The estimates in the present study need not agree with a particular previously reported value since these were obtained in different populations under different environmental conditions and often by different types of analysis but the previous estimates provide a useful reference.

The summary of daily gain indicates that the effects of farm by season interactions are probably the most serious cause of upward bias in estimating the additive genetic variance for gain. The fact that the removal of the average farm influences does not change the estimate of heritability appreciably, while the removal of farm by season interactions drastically reduces the estimate, supports this conclusion. The small numbers in the analysis of farm by season interactions must be considered. The last two estimates of heritability in gain from Table 18 agree reasonably well with those in the literature.

Table 18. Summary of estimates of genetic variance and heritability

Reference	Method of estimation	Genetic variance Expectation[a]
Table 8	$\frac{1}{2fxy} S$	$\sigma^2_A + \ldots + CF + F$
Table 12	$\frac{1}{2fxy} CF$	$\sigma^2_A + \ldots + CF$
Table 15	$\frac{1}{2fxy} S$	$\sigma^2_A + \ldots + F$
Table 8	$\frac{1}{.5-2fxy} D$	$\sigma^2_A + \ldots + \sigma^2_M$
Table 17	Least squares	$\sigma^2_A + \sigma^2_D + \ldots$

Reference	Gain			Probe		
	Genetic[b] variance	Phenotypic variance	Heritability	Genetic[b] variance	Phenotypic variance	Heritability
Table 8	.0219	.0376	.58	.0303	.0303	1.00
Table 12	.0252	.0387	.65	.0122	.0247	.49
Table 15	.0029	.0391	.07	.0222	.0281	.79
Table 8	.0058	.0376	.25	.0416	.0303	1.68
Table 17	.0111	.0332	.33	.0400	.0340	1.18

[a]The exact formulation of the expectations are given in conjunction with the tables cited.

[b]The method of estimation and the expectations of the genetic variance are given in the upper part of this table.

The results for probe summarized similarly in Table 18 differ from the gain in that probe shows a considerable general farm influence in addition to the farm by season interaction. These farm differences increase the differences between the paternal sib groups and are confounded with various estimates of genetic variance. The reason for the large dam component found in the analysis of probe is not obvious. Previous work gives little justification to the idea that maternal influences play an important role in the more highly heritable carcass characteristics such as backfat thickness.

The size of the farm differences in probe raises the question of the extent to which these differences are due to genetic differences between farms. An interesting speculation is that these may be largely genetic differences caused by varying emphasis on backfat in the selection programs of the individual breeders during the rather recent trend toward leaner swine.

The environmental, genetic and phenotypic covariances and respective correlations between gain and probe are summarized in Table 19. The covariances and variances ascribed to the various forces were computed from the variance and covariance components of the analyses. The approach allows a calculated variance to be negative which is logically impossible and, of course, precluded estimating the correlation in such cases. The values indicate rather clearly a positive phenotypic correlation between these two traits and this has been well recognized in previous literature. The value of the genetic covariance

Table 19. Summary of estimates of the covariance between gain and probe and the respective correlations

Reference	Method of estimation	Expectations[a]
Table 8	(1/2 fxy) Cov S	$\sigma_{A_1A_2} + \ldots + AF + F$
Table 12	(1/2 fxy) Cov S	$\sigma_{A_1A_2} + \ldots + AF$
Table 15	(1/2 fxy) Cov S	$\sigma_{A_1A_2} + \ldots F$
Table 17	Least squares	$\sigma_{A_1A_2} + \sigma_{D_1D_2} + \ldots$

	Genetic		Environmental		Phenotypic	
	Cov.	rgg	Cov.	ree	Cov.	rpp
Table 8	.0090	.35	-.0002	[b]	.0088	.26
Table 12	.0097	.59	-.0011	-.08	.0092	.28
Table 15	.0103	1.28	-.0056	-.38	.0047	.14
Table 17	.0116	[b]	.0110	[b]	.0165	.54

[a]The exact formulation of the expectations are given in conjunction with Tables Cited.

[b]Negative estimates of components of variance prevent estimating the correlation.

is positive in all cases and the genetic correlation is larger than the corresponding phenotypic correlation. A negative environmental correlation is indicated where the estimate was possible.

F. Discussion of Results

A central purpose of the testing station program is to aid the intra-breed genetic improvement in the economic characteristics of swine. The efficiency of various testing schemes in accomplishing this aim was studied by Smith (1958). He concluded that little direct genetic improvement can be expected from a testing system organized as it is in Iowa. This is the result of the manner in which the testing system is integrated with the structure of the swine population. Many tested individuals are now sold directly to commercial breeders which allows little accumulation of genetic merit in the purebred herds. Smith (1958) proposed that a more efficient system would result if only a few elite herds tested their animals and the purebred breeder multiplied the stock from these elite herds for use by commercial swine producers. Indirectly the testing system may have a large effect on the genetic composition of the population when the testing stations are used as an educational tool and serve to set well-defined goals in swine improvement.

Presumably, the rather homogeneous and standard environment at the central testing station allows a more accurate comparison of the genotypes of the individuals on test. The testing station would ideally reduce the environmental portion of the differences between the elite herds. The present study has shown that pre-test environments are probably carrying over into the results of the tests and contributing to the differences between sire groups. The factors which remain constant over several seasons but which vary between farms apparently contribute to sire differences in probe while sire differences in daily gain are

probably inflated largely by conditions peculiar to a given farm and season.

Changes in the testing system could be made to assess the contribution of the pre-test environments more accurately. Breeders could submit two entries each season and differences between sires from the same farm and in the same season could be compared with sire differences between farms. This would halve the number of breeders who would be able to use the testing facilities and unless the testing was restricted to a few elite herds or available facilities were extensive such a scheme would probably reduce the efficiency of the system. The differences between farms in the average probe is probably partly genetic and, as such, should not be removed from the test results by any adjustment directed at reducing environmental differences.

Testing groups of half sibs from the same sire over two or more seasons could be employed to assess the importance of the interaction of farm environments and genotypes with the seasons. Perhaps testing groups of half sibs over farms and stations in diverse locations might be more appropriate than central testing if genotype by environmental interactions are important sources of variation.

If the optimum system of testing is where a small nucleus of herds tests stock for use in purebred multiplier herds then testing the sons of tested sires would not be possible since the sons would not be found in the elite herds. Other systems of testing could employ methods to obtain parent-offspring relationships and provide a further method of assessing genetic influence in these traits.

The decline in probe over the five seasons is one of the strongest trends in the study. On the average the live probe decreased -0.14 inches of fat from one testing period to another. The change has probably been the result of the emphasis on leaner swine incorporated in many extension programs. The use of the live probe by individual farmers which could improve the selection of pigs for testing and actual genetic changes in the population are probably responsible for most of this trend. The decline in probe has been paralleled by a less distinct downward trend in daily gain. This change was not unexpected considering the strong positive phenotypic correlation between daily gain and probe evident in all the analyses. The correlation seemed to be almost wholly genetic with some faint indication the environmental portion was negative. The decline in gain of the various breeds has not been the same and the differences between breeds in this time trend appears important. It is not possible to completely isolate the cause of this differential time trend in the breeds. It has followed a shift in testing procedures from pens of three to pens of four pigs and competition effects could be a contributing factor. The conclusion that pen differences were not important was made when the older system of three individuals per pen was in use. Possibly differences between pens would become important when individuals are put under the greater stress of crowded conditions.

The problem of a genetic antagonism between two desirable traits is not new to plant and animal breeding. While the difficulty is common the remedy is not always evident although the approach to the problem

through a selection index offers a logical solution. The recent promotion of the meat type hog and the advent of the mechanical live probe has increased emphasis on decreasing the depth of backfat since this measure is highly correlated with lean cut percentage. The genetic parameters estimated in this study indicate the need to consider the effect that selection for lean carcasses will have on daily gain.

VI. SUMMARY

The nature and extent of the genetic and environmental influences controlling the variation in daily gain and live probe on swine tested under the management of a central station were studied using the data from five seasons of testing by the Iowa Swine Testing Association. The information was from 1266 boars and 467 barrows representing nine breeds.

The average change in the two traits from one period to another over the five seasons was -0.07 pound of gain and -0.14 inches of backfat. Considerable season and breed variation was present. The differential time trend in daily gain among the breeds was evident.

The variation within breeds and seasons was studied largely by analyzing the genetic and environmental correlations in the paternal sib correlation. Since each entry or paternal sib group was submitted by a different breeder, pre-test farm influences were confounded with the genetic differences among half sibs. The estimate of intra-breed and season heritability of probe was reduced from 1.00 to 0.49 when the average farm influences were included in the model and thus removed from the paternal sib component. The farm differences in probe were probably partly and could have been largely genetic. The estimate of intra-breed and season heritability of gain did not appear to be influenced by average farm effects but was reduced from 0.58 to 0.07 when the influences of the farm environments peculiar to a given season were first removed from the sire component. The genetic covariance between gain and probe was positive in all the variance analyses and was little

influenced by removing pre-test farm environmental factors from the paternal sib component of covariance. The genetic correlation between gain and probe within farm was 0.59 and the phenotypic correlation was 0.28.

Individual comparisons based on the relationship existing in each pen were studied to estimate the genetic covariance between individuals free of farm and other pre-test influences. The variance components obtained in this manner for gain were in reasonable agreement with other estimates while those concerning probe included negative estimates of environmental variance. Further estimation of components of epistatic variance was theoretically possible but highly impractical with the data available. The small range of relationships gave rise to conditions where the solutions of the normal equations was hampered by an almost singular situation in the matrix of coefficients. The genetic covariance between gain and probe was studied in a similar manner and, when maternal influences were included, gave values essentially in agreement with previous estimates in this study.

The considerable emphasis on lean swine has been apparently effective in reducing the average backfat on pigs sent to the testing station. The size and sign of the genetic correlation between gain and probe stresses the need for considering these traits jointly in a selection program. The important contribution of the farm environments to the paternal sib correlation should be considered in using the test results as a reflection of genetic merit.

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